

## BEE FAUNA ASSOCIATED WITH SHRUBS IN TWO CALIFORNIA CHAPARRAL COMMUNITIES

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*Abstract.*—The bee faunas visiting spring-blooming shrubs in the chaparral of northern California were compared between two localities having similar plant species but different climatic regimes. Bees were collected from mid-March to mid-July during two consecutive years that were characterized by different rainfall. In the Inner Coast Ranges of Napa County, with a mediterranean climate, 73 bee species from six families were recorded on 11 shrub species; Megachilidae was the most species-rich family, followed by Andrenidae and Halictidae. Immediately inland from the coast in Marin County, where the frequently cool, foggy conditions are unfavorable for many solitary bees, the bee fauna had only half the number of species and a third the number of individuals; there were very few Megachilidae and a relatively high abundance of bumble bees. Of the 81 total species at both sites, close to one-third were shared between sites; the introduced honey bee was ubiquitous. A greater number of species were collected during the year of normal rainfall, most species were recorded in low abundance, and females comprised two-thirds of the collected specimens. Shrubs of the genus *Ceanothus* attracted the greatest diversity of bees. Comparison with other regional bee surveys shows the inland site here to be most typical of other areas with chaparral.

*Key Words.*—Insecta, Apoidea, Hymenoptera, faunal survey, chaparral, pollination, California

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Surveys of pollinators in different plant communities of California show the chaparral community to have the largest diversity of bee species per area, as well as comparatively high diversities of other flower-visiting insects (Moldenke 1976a). Furthermore, these studies indicate that bees are the most species-rich group of pollinators throughout California, with the exception of subalpine marsh meadows. Bees are typically most diverse in warm temperate xeric climates (Michener 1979). Within California, the southern deserts and mediterranean-climate regions have the highest number of species, with up to three-fold more than alpine, Great Basin, and immediate-coastal areas (Moldenke 1976a, 1979a). This concentration in arid regions may be attributed, in part, to the generally high diversity of plants blooming during the short flight season of bees, and to the tendency of most solitary bees to nest in the ground, where risk of mortality from fungus attacks is decreased in dry climates (Linsley 1958, Michener 1979). In the chaparral community, bees are the most significant pollinators; in terms of abundance, they outnumber all other flower-visiting insects except beetles, whose greatest impact is, however, as flower herbivores (Moldenke 1976a).

The chaparral vegetation covers large areas of California and occurs inland from the coast, mainly within the Coast Ranges and at low- to mid-elevations bordering the Central Valley, especially on dry rocky slopes with thin soil (Munz & Keck 1959, Keeley & Keeley 1988). These regions are characterized by a prevailingly mediterranean-type climate with hot dry summers and cool wet winters, but chaparral may also extend into areas with more moderate climatic regimes. Chap-

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arral is dominated by evergreen sclerophyllous, fire-adapted shrubs, which commonly include *Adenostoma fasciculatum* Hooker & Arnott (chamise), *Ceanothus* spp., and *Arctostaphylos* spp. (manzanita); the herbaceous cover is generally sparse except during the first years following fire (Hanes 1977, Keeley & Keeley 1988). In mature chaparral, flowering shrubs comprise the major food source for bees, although herbaceous plants growing in shrub openings or neighboring grassland appear to play a role in maintaining populations of certain bee species (Dobson 1980). The principal blooming season follows the winter rains, with most shrub species flowering between March and June (Moldenke 1979b). This corresponds to the period in spring when both soil moisture is still plentiful and ambient temperatures have increased to levels favorable for insect activity, but before the hot, dry summer begins; this is also the time when most insects, including flower visitors, reach peak numbers (Force 1990).

This paper compares the species composition and relative abundance of bees collected on the flowers of spring-blooming shrubs in two chaparral sites in northern California. The sites were chosen for their ease of accessibility and generally similar shrubby flora; they differed in climate, with the site closer to the coast being cooler and subject to frequent fog. Data on the bee fauna were gathered for two consecutive years characterized by sharply different amounts of rainfall. The results here represent part of a broader study of the pollinator and flower-visiting insect fauna associated with chaparral shrubs (Dobson 1980). In addition to increasing our understanding of insect-plant interactions in the chaparral, this study had the goal of providing baseline data for future faunal surveys and to serve in efforts to preserve the California chaparral community.

#### METHODS AND MATERIALS

The study was carried out at two chaparral sites, 50 airline km apart, in northern California. The first site was located in the Inner Coast Ranges of Napa County, on the upper east-facing slope of Mt. Veeder at 550 m elevation. The vegetation consisted principally of mature impenetrable chaparral, interspersed with stands of mixed evergreen forest, but within the study plot (approximately 200 m<sup>2</sup>) the chaparral was more open, having been cleared mechanically 4 years previously; herbaceous plants were sparse. The second site was situated in the Outer Coast Ranges in Marin County, at the foot of Pine Mountain at 335 m elevation, facing south over Alpine Lake. Due to the closer proximity of the ocean (within 12 airline km), the spring-summer climate is cooler and windier than on Mt. Veeder, with frequent fog, especially in the mornings. The study plot, of similar size as the previous, was in an area where the strongly serpentine character of the soil yielded an open plant cover comprised of low-growing shrubs, which included serpentine-endemic species.

Bees visiting the flowering shrubs were censused at each site 1 day per week during the spring-summer months, from mid-March to mid-July in 1977 and 1978, using sweep-net collection methods. Collecting was concentrated on selected shrubs of each species, which were sampled in succession over 30 min periods every 2–3 h, from 08:30 h to 16:30 h, thus spanning the daytime hours of bee activity. Hourly recordings of ambient temperature were taken during each sampling day in 1978. Based on the collected specimens, bee faunas were compared between sites with respect to the numbers and kinds of species, relative abun-



dances, sex ratios, and Shannon-Wiener diversity indexes of individual families, temporal activities, and shrub associations. Some species, particularly fast-flying bees (e.g., large Anthophoridae), were difficult to collect and, therefore, are underrepresented in the samples. The introduced honey bee, which was very common on certain shrubs, was not collected in proportion to its abundance and was censused mainly for its presence. Bee specimens were identified by specialists and vouchers deposited in the R. M. Bohart Museum of Entomology, University of California, Davis.

## RESULTS

*Habitat Resources.*—During the study a total of 13 shrub species from seven families bloomed at the two sites: 11 at Mt. Veeder and eight at Pine Mountain; six of the species occurred at both sites. Following the nomenclature of Munz & Keck (1959), shrubs common to the sites were *Eriodictyon californicum* (Hooker & Arnott) Torrey (Hydrophyllaceae), *Pickeringia montana* Nuttall (Leguminosae), *Rhamnus californica* Eschscholtz (Rhamnaceae), *Adenostoma fasciculatum* and *Heteromeles arbutifolia* M. Roemer (Rosaceae), and *Mimulus (Diplacus) aurantiacus* Curtis (Scrophulariaceae); only at Mt. Veeder: *Arctostaphylos viscida* Parry (Ericaceae), *Dendromecon rigida* Bentham (Papaveraceae), *Ceanothus foliosus* Parry, *C. parryi* Trelease, and *C. sonomensis* J. T. Howell (Rhamnaceae); and only at Pine Mountain: *Arctostaphylos pungens* var. *montana* (Eastwood) Munz and *Ceanothus jepsonii* Greene. With the exception of *Dendromecon*, all genera were represented at both sites. Thus, any taxonomic differences between sites were at the species level.

Blooming phenologies of the shrubs were generally similar both years, but flower density was less in 1977. This was especially marked for *R. californica*, *P. montana*, and *A. fasciculatum* (produced no flowers); *C. parryi* on Mt. Veeder was unusual in producing a denser bloom in 1977. The two study years differed markedly in rainfall, and this was most pronounced in the more inland site on Mt. Veeder. During 1977, which was the second of two consecutive years with severe drought, precipitation was several fold less than in 1978, which received slightly above normal rainfall. For each weather year (1 Jul–30 Jun), rainfall at Mt. Veeder was 32.94 cm (1977) and 117.07 cm (1978), with an average over 33 years of 82.96 cm (data from Oakville, Napa Co., National Weather Service 1948–1981); at Pine Mt., rainfall was 56.74 cm (1977) and 170.21 cm (1978), with an average over 113 years of 131.47 cm (data from Lake Lagunitas, Marin Co.; Roxon 1992).

*Bee Species.*—A total of 81 bee species, representing six families, were collected on the 13 shrubs at the two sites (Appendix 1). Mt. Veeder had 73 species, and thus twice as many as Pine Mountain, with only 36 species (Table 1). With the exception of Halictidae, which had an equal number of species at both sites, species numbers within each family were greater at Mt. Veeder; this was most pronounced in Megachilidae, where differences between sites reached ten-fold.

Approximately one-third of the species were collected at both sites (Table 1 and Appendix 1). This shared bee fauna constituted a high proportion (78%) of the species at Pine Mountain, but only a third (38%) of those at Mt. Veeder; Halictidae, which was the most species-rich family at Pine Mountain, contributed the largest number (10 of 28 species). Of the 53 species collected exclusively at

Table 1. Number of bee species collected at each site and number shared by (common to) both sites.

Family	Mt. Veeder				Pine Mtn.				Shared
	Only 1977	Only 1978	Both 1977/1978	Total 1977 + 1978	Only 1977	Only 1978	Both 1977/1978	Total 1977 + 1978	
Andrenidae	3	4	8	15	3	5	1	9	6
Anthophoridae	0	4	4	8	1	0	2	3	2
Apidae	0	2	4	6	0	0	4	4	4
Colletidae	0	4	5	9	0	3	2	5	5
Halictidae	0	7	6	13	2	7	4	13	10
Megachilidae	3	7	12	22	1	1	0	2	1
Sum	6	28	39	73	7	16	13	36	28
%	8.4	38.4	53.4	100.0	19.4	44.4	36.1	100.0	

one site, 45 were at Mt. Veeder and, among these, close to 50% were Megachilidae and 20% Andrenidae.

A larger number of bee species were collected in 1978, when rainfall was normal, than in 1977, a year of drought (Table 1). Both sites showed relative increases of close to 50% from 1977 to 1978. Species exclusive to 1978 included a large proportion of the small and mainly late-spring active bees (e.g., Colletidae, Halictidae, and *Ceratina* in Anthophoridae). The majority of species collected in 1977 were recorded both years. These more constant bees, which represented the most stable component of the fauna, comprised approximately half the species at Mt. Veeder and a third of those at Pine Mountain.

*Bee Relative Abundance.*—During the two years, 799 bee specimens were collected at Mt. Veeder and 205 at Pine Mountain (Table 2). Most species were low in abundance (Appendix 1). Based on apparent breaks in the numbers of species distributed in function of their abundance, 54% of species at Mt. Veeder can be classified as rare (1–4 specimens each), 26% occasional (5–15 specimens), 14% common (20–32 specimens), and 6% abundant (48–96 specimens). Abundant species consisted of *Andrena chlorura* Cockerell and *A. vandykei* Cockerell (Andrenidae), *Bombus edwardsii* Cresson (Apidae), and *Hylaeus polifolii* (Cockerell) (Colletidae). The pattern at Pine Mountain was very similar, with 57% of species rare (1–2 specimens), 23% occasional (3–6 specimens), 14% common (8–14 specimens), and 6% abundant (21–37 specimens). The latter included *Panurginus nigrellus* Crawford (Andrenidae) and *H. polifolii*.

Table 2. Bee abundance (number of specimens collected) at each site over both years.

Family	Mt. Veeder				Pine Mtn.			
	♀	♂	Total	% ♂	♀	♂	Total	% ♂
Andrenidae	219	26	245	10.6	18	24	42	57.1
Anthophoridae	37	20	57	35.1	5	0	5	0.0
Apidae	101	42	143	29.4	50	5	55	9.1
Colletidae	40	113	153	73.9	14	37	51	72.5
Halictidae	83	7	90	7.8	30	20	50	40.0
Megachilidae	76	35	111	31.5	1	1	2	50.0
Total	556	243	799	30.4	118	87	205	42.4



Table 3. Representation of each family in terms of species and specimen numbers, and family diversity index  $H'$ .

Family	Mt. Veeder			Pine Mtn.		
	% total species	% total specimens	$H'$ <sup>a</sup>	% total species	% total specimens	$H'$ <sup>a</sup>
Andrenidae	20.5	30.7	1.88	25.0	20.5	1.60
Anthophoridae	11.0	7.1	1.63	8.3	2.4	1.05
Apidae	8.2	17.9	0.92 <sup>b</sup>	11.1	26.8	0.99 <sup>b</sup>
Colletidae	12.3	19.1	1.71	13.9	24.9	0.88
Halictidae	17.8	11.3	2.06	36.1	24.4	2.18
Megachilidae	30.1	13.9	2.77	5.6	1.0	0.69

<sup>a</sup> Shannon-Wiener diversity index, where  $H' = -\sum p_i \ln p_i$ , and  $p_i$  = proportion of total specimens in a family that belong to the  $i$ th species (Whittaker 1972).

<sup>b</sup> Excluding the introduced honey bee, *Apis mellifera*.

The proportion of males collected varied among families and between sites (Table 2). Colletidae had an exceptionally high percentage of males (over 70%) at both sites, whereas most other families had a marked predominance of females. In Andrenidae and Halictidae, males and females tended to be more equally represented at Pine Mountain.

*Bee Faunal Composition.*—In terms of species numbers, each site was dominated by a single family (Table 3). Megachilidae (with 30% of the species) were dominant at Mt. Veeder and Halictidae (36%) at Pine Mountain. Figures for other families were generally similar between sites, with Andrenidae occupying second place. Pine Mountain had a striking paucity of Megachilidae (5.6%).

With respect to relative abundance (Table 3), Andrenidae were clearly the most abundant bees at Mt. Veeder, whereas no family predominated at Pine Mountain. Anthophoridae were few at both sites. Overall, the sites differed in the comparatively high relative abundance of Andrenidae at Mt. Veeder and the low abundance of Megachilidae at Pine Mountain.

The Shannon-Wiener diversity index of each family, which is based on both the number of species and the relative abundance of each species (Whittaker 1972), provides a measure of how equitably the species are represented within each site (Table 3). Megachilidae had the highest diversity at Mt. Veeder, followed by Halictidae, whereas at Pine Mountain Halictidae was highest. Index values at Mt. Veeder clearly exceeded those at Pine Mountain for Megachilidae, Colletidae, and Anthophoridae.

*Temporal Activity of Bees.*—Daily activity levels, based on the number of specimens collected at bihourly intervals, were generally uniform among families and between sexes. At Mt. Veeder, bee activity showed a normal distribution, with a maximum around midday. This corresponded with, or slightly preceded, the time of highest daily ambient temperature between 13:00 and 15:00 h. Diverging activity patterns were evident in four cases: (1) female Megachilidae, with a generally high activity over the morning hours; (2) female Andrenidae, with peak activity during mid-morning; (3) male Colletidae, with maximum activity extending broadly from mid-morning to mid-afternoon; and (4) male Apidae (*Bombus*) and Anthophoridae (excluding *Ceratina*), with a bimodal activity curve showing a small peak in early morning and a principal peak at midday.

Seasonal activity patterns of bee families, measured by the number of species collected over the course of the study, were in general similar at the two sites. As exemplified by Mt. Veeder (Fig. 1), Andrenidae flew almost exclusively during the early part of the spring, Megachilidae reached peak activity during the middle period, and Colletidae, with initially very low activity, increased across the season; Halictidae, Apidae, and Anthophoridae maintained relatively constant levels throughout the study. Considering all families together, the total number of species was quite uniform and showed only a moderate peak in early spring, associated primarily with the blooming of *Ceanothus*, and a smaller one at the end of the season, on *Heteromeles*.

*Bee-shrub Associations.* — A list of bee species collected on each shrub genus at each site is provided in Appendix 1; bee-shrub associations at Mt. Veeder are broken down by bee family in Fig. 1. The number of bee species per shrub genus ranged from 4–33 at Mt. Veeder and 2–16 at Pine Mountain. At Mt. Veeder, *Ceanothus* (33 species) received the greatest number, followed by *Heteromeles* (27 species), *Eriodictyon* and *Pickeringia* (each 23 species); *Dendromecon* (four species), which is nectarless, received the fewest. A major contrast between sites was the paucity of bees on *Mimulus* and *Pickeringia* at Pine Mountain, whereas at Mt. Veeder these shrubs attracted numerous species, especially Megachilidae. At Mt. Veeder each shrub genus was visited by at least three of the six bee families; all families were represented on *Ceanothus* and *Eriodictyon*.

Bee-shrub associations showed greater diversity at Mt. Veeder. Bees recorded at both sites generally visited more shrub taxa at Mt. Veeder and most bee-shrub associations at Pine Mountain were likewise observed at Mt. Veeder. At the bee family level, Halictidae and Apidae showed the broadest associations, which spanned all shrub genera, and Andrenidae exhibited the most restricted visitation. At the bee species level, Andrenidae tended to visit principally *Arctostaphylos* and *Ceanothus* shrubs. The majority of species in other families showed more generalist foraging patterns, with several host shrubs each. Flower and pollen specificity at Mt. Veeder are discussed in greater detail in Dobson (1980).

*The Introduced Honey Bee.* — Honey bees were frequent at both sites and foraged throughout the day from early morning to late afternoon, utilizing floral resources over longer daily periods than most native bees except *Bombus*. At Mt. Veeder, they visited all shrubs except *Mimulus*; they were the most abundant bees on *Arctostaphylos* and the tree *Arbutus menziesii* Pursh (madrone, Ericaceae), both of which bloomed in early spring during the major population growth of honey bee colonies, and on *Rhamnus* and *Heteromeles*, which were the last nectar-providing shrubs to bloom. At Pine Mountain, honey bees accounted for the majority of visitors on five of the seven shrub species and seemed to occupy a foraging niche generally similar to that of bumble bees.

Although no remarkable interferences in foraging were observed among any of the native bees, several instances of negative interactions were recorded between honey bees and native bees, especially at Mt. Veeder where solitary bees were most abundant. During these encounters, which occurred mainly on *Rhamnus* and *Heteromeles*, honey bees either actively chased small bees away from flowers or caused them to fly off upon landing on the same flower or inflorescence. Individual shrubs heavily frequented by honey bees appeared to have distinctly



## Mt. Veeder

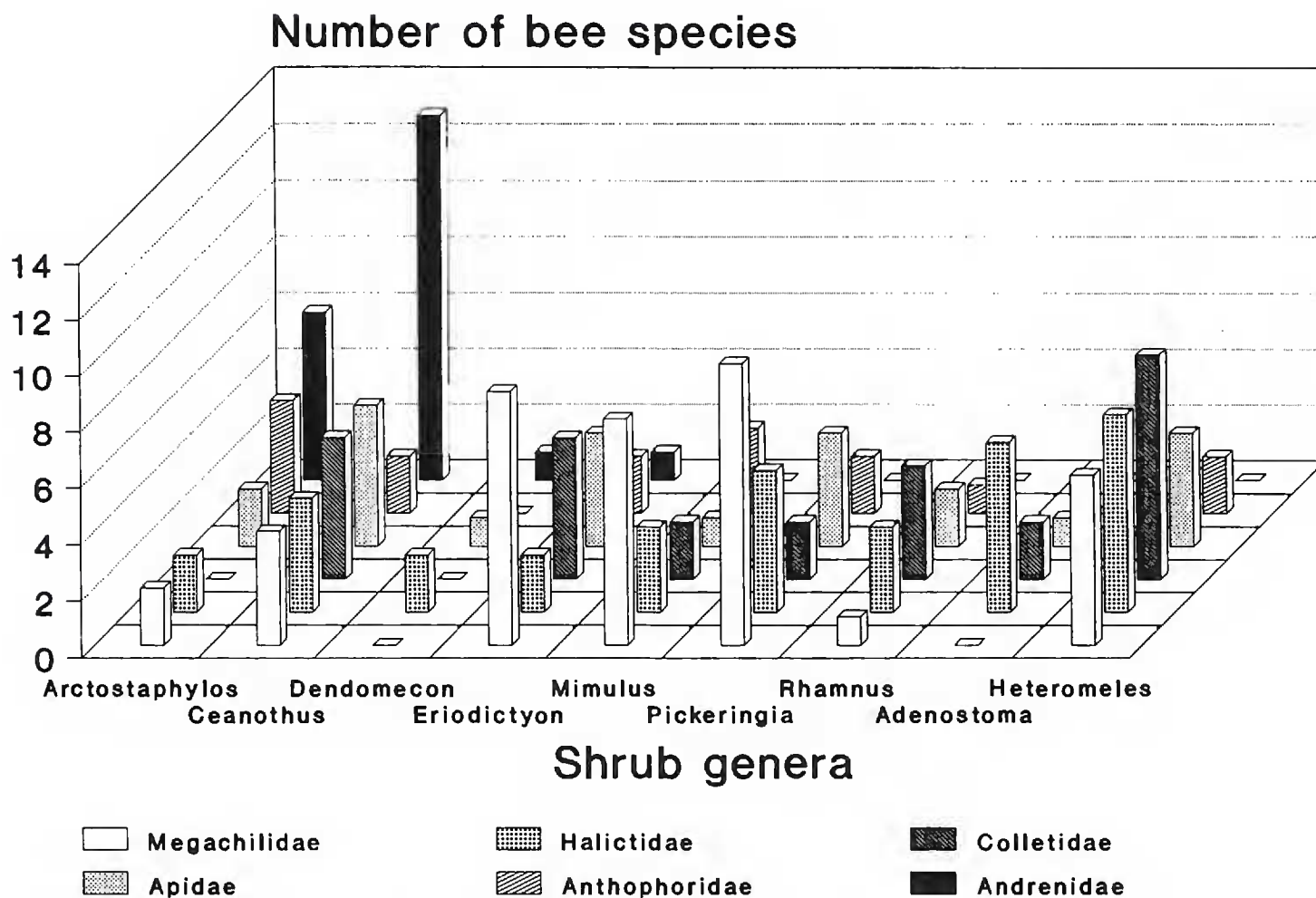


Figure 1. Number of bee species in each family that were collected on the different shrub genera, Mt. Veeder, 1977 and 1978. Shrubs are arranged according to the seasonal chronology of their peak blooming periods.

fewer solitary bees compared to other shrubs, but no count data were collected to verify this impression.

### DISCUSSION

The two chaparral sites were found to have bee faunas that differed sharply in both numbers of species and abundance, even though the shrub floras were similar. With twice as many species of bees and over three-fold more bee specimens, the Mt. Veeder site, situated in the warm and dry Inner Coast Ranges, had a much more diverse bee fauna, as is also reflected in the higher diversity indexes within its bee families. The cooler and more coastal climatic conditions (frequent fog and winds) at the Pine Mountain site, located just inland from the coast, appeared to be a major factor limiting its bee fauna, thereby overriding intersite similarities in the composition of bee host-plants. Likewise, the presence in northern California of comparatively few flower-visiting insects on the immediate coast at Point Reyes, compared to a chaparral site at Jasper Ridge, has also been attributed to the restrictions imposed by the foggy, cool, and windy coastal climate (Moldenke 1975).

Parallel decreases in bee fauna associated with proximity to the coast have been documented in other areas. In California, reductions of 50% in bee species, as well as in total pollinator diversity, may occur in coastal communities compared

to adjacent chaparral (Moldenke 1976a), and differences of the same magnitude have been recorded between vegetationally similar (but floristically different) coastal and inland sites in scrubby mediterranean-climate areas of southern Spain (Herrera 1988) and Chile (Moldenke 1979b, c). These changes in bee species are, however, not surprising, given the general tendency of bee numbers to increase as one moves into comparatively warmer, more xeric habitats (Linsley 1958, Michener 1979, Dylewska 1988, Armbruster & Guinn 1989).

Moldenke's (1976a) observations that the pollinator fauna of northern coastal scrub shifts to a depauperate chaparral fauna inland of the immediate coast are corroborated here, where almost 80% of the species at Pine Mountain were also found at Mt. Veeder. Nevertheless, of the total species at Mt. Veeder, only 23% included the chaparral community among their list of characteristic habitats (Moldenke & Neff 1974a); the majority belonged to Andrenidae and Megachilidae, the two most species-rich families at the site. The corresponding figure at Pine Mountain was 22%, with the species distributed among several families. According to geographic and habitat distributions listed for 66 of the 81 species at the two sites (Moldenke & Neff 1974a), 61 species are wide-ranging and occur mainly in montane regions of both northern and southern California, and five are principally southern Californian species.

In terms of bee faunal compositions, the most striking contrast between sites was the high percentage of Megachilidae species at Mt. Veeder, which supports reports that this family is generally well represented in the scrubby vegetations of California but is less prevalent in other habitats, including coastal areas (Moldenke 1976a). A second contrast was the high percentage of Halictidae at Pine Mountain. Comparison with bee faunas in other chaparral and coastal communities in California (Table 4) shows that both sites resemble others in their percentage of species in Andrenidae (high), but are distinctive in having figures that are higher for Colletidae and lower for Anthophoridae. These differences may arise partly from the study being restricted in time (i.e., to spring-summer months) and in habitat (i.e., to shrubby plants). Similarly affected was the total number of recorded species: at Mt. Veeder this was very low compared to other chaparral sites; at Pine Mountain it was somewhat lower compared to the other coastal areas. Discrepancies specifically in the number of Anthophoridae may result from the under-collection of fast-flying species as well as the lack of revisionary studies of *Nomada* (resulting in many undescribed species) which, while accounting for the largest proportion of Anthophoridae species in Moldenke (1976b), were collected in only low numbers here. Comparisons in the Apidae, Halictidae, and Megachilidae, however, suggest that Mt. Veeder is more typical of chaparral and Pine Mountain of coastal habitats. Indeed, Mt. Veeder resembled the chaparral regions in its unusually high percentage of Megachilidae (around 30%) and somewhat low percentage of Halictidae (under 20%), whereas Pine Mountain displayed in extreme the coastal sites' opposite trends and a moderate tendency for higher proportions of Apidae.

Relative abundance of each family did not closely follow patterns in species numbers, and the greatest deviations occurred at Mt. Veeder in Apidae, with few species but high abundances, and Megachilidae, with many species comprised of few individuals each. The distribution of specimen numbers across the species was very similar at the two sites; the majority of species (80%) had low relative



Table 4. Family representations of bee faunas (% total species) at various localities with chaparral or coastal vegetation in California.

Family	Chaparral vegetation						Mixed Channel Islands <sup>c</sup>	Coastal vegetation			
	Mt. Veeder	Pine Mtn.	N. coast range <sup>a</sup>	Mather <sup>b</sup>	Echo Valley <sup>c</sup>	Japatul Valley <sup>d</sup>		N. coast <sup>f</sup>	Bodega <sup>g</sup>	Hum- boldt <sup>h</sup>	S. coast <sup>i</sup>
Andrenidae	20.5	25.0	18.3	21.5	20.1	18.5	20.3	20.4	17.0	9.3	28.4
Anthophoridae	11.0	8.3	28.1	22.2	28.4	20.5	32.0	25.3	25.5	11.6	32.1
Apidae	8.2	11.1	2.9	4.2	1.2	1.3	4.6	6.2	17.0	25.6	2.4
Colletidae	12.3	13.9	4.2	7.6	5.3	2.0	1.3	6.2	4.3	7.0	1.2
Halictidae	17.8	36.1	16.2	15.3	19.5	19.2	24.8	26.5	21.3	23.3	22.2
Megachilidae	30.1	5.6	30.2	29.2	24.9	37.7	17.0	14.8	14.9	23.3	11.1
Melittidae	0	0	0	0	0.6	0.7	0	0.6	0	0	2.4
No. species	73	36	377	144	169	151	153	162	47	43	81

<sup>a</sup> Jasper Ridge, San Mateo Co. (Moldenke 1976a).

<sup>b</sup> Sierra Nevada foothills, Tuolumne Co. (Moldenke & Neff 1974b).

<sup>c</sup> San Diego Co. (Moldenke & Neff 1974b).

<sup>d</sup> Post-fire (mainly annual flora), San Diego Co. (Moldenke & Neff 1974b).

<sup>e</sup> Mainly chaparral and coastal scrub/prairie (Rust et al. 1985).

<sup>f</sup> Coastal scrub, Point Reyes, Marin Co. and Pescadero, San Mateo Co. (Moldenke 1976a).

<sup>g</sup> Dunes and prairie, Sonoma Co. (Thorp & Gordon 1992).

<sup>h</sup> Dunes, Humboldt Co. (Thorp & Gordon 1992).

<sup>i</sup> Coastal scrub, Torrey Pines, San Diego Co. (Moldenke & Neff 1974b).

abundances, and only 6% were exceptionally numerous. The patterns corroborate general trends of plant and animal surveys, in which species-abundance curves typically show logarithmic distributions (Preston 1948, Tepedino & Stanton 1981).

Bees were most numerous, in both species and individuals, during the year of normal rainfall, when plant bloom was denser and all shrub species flowered. The substantial increases in species numbers that occurred at both sites from the year of drought (1977) to the year of normal rainfall (1978), amounting to almost half of the total species recorded, indicates that bee diversity during a given year is not simply a function of the previous year's bee fauna. Indeed, it suggests that some bee species are parsivoltine, in which individuals of a single species require different numbers of years to complete development or emerge from the nest. Parsivoltinism has been documented in several bees, especially Megachilidae, and studies of *Osmia* species suggest that this polymorphism in emergence time is genetically controlled (Torchio & Tepedino 1982). However, it cannot be excluded that in other cases emergence may be cued to rainfall patterns and that during unfavorable years bees may remain dormant in their nests until a more favorable season (Linsley 1958). This may apply to Mt. Veeder, where most of the bees collected exclusively during the year of normal rainfall were species that fly in mid-spring to summer when any water shortage effects might critically restrict bee activity. The triggering of bee emergence by moisture levels has been proposed especially in relation to desert bees that were observed to fly only when water was sufficient for their primarily annual host plants to germinate and bloom (e.g., Linsley 1978).

The few bee species recorded exclusively during the drought year may represent bees that extended their foraging ranges into neighboring habitats or onto alternate host plants (i.e., chaparral shrubs) to supplement the decreased availability of

their usual food plants. The yearly variation in floral resources observed in this study does not appear to be very unusual in plant communities (e.g., Rotenberry 1990, Tepedino & Stanton 1980). Furthermore, the corresponding changes in the bee fauna lend support to Tepedino & Stanton's (1981) contention that a large proportion of the occasional bees within a fauna may be opportunistic fugitives that respond to the spatiotemporal unpredictability of floral resources by dispersing among patchily distributed food sources. Given the comparatively great variance in annual rainfall, common occurrence of drought, and year-to-year variation in flower production within the chaparral (Keeley & Keeley 1988), the differences in bee faunal compositions obtained over the 2 years here could be viewed as typical of chaparral communities.

The differing composition and abundance of bee species at the two sites probably stemmed primarily from the influence of climatic conditions on bee activity, although availability of nesting sites and density of host-plant bloom may have also played a role. The warmer, drier, and more constant spring-summer weather at Mt. Veeder provided more hours during the day and days during the season that were favorable for bee activity than at Pine Mountain and thereby allowed for a larger number of solitary bees. Most of the species collected exclusively at Mt. Veeder were small-bodied or metallic-colored bees (e.g., *Hylaeus*, *Osmia*, *Ceratina*), which generally require higher ambient temperatures for flight than do larger-sized bees (Stone & Willmer 1989). Unsurprisingly, in the changing climate at Pine Mountain the abundance and diversity of bees on the shrubs fluctuated often hourly in relation to the weather. During the frequent, cool periods of fog and winds, activity decreased sharply and only honey bees and bumble bees continued to forage. These large hairy bees, particularly *Bombus*, can generate and maintain higher body temperatures under adverse ambient conditions (Heinrich 1979, Stone & Willmer 1989) and were the most abundant bees at this site. In addition, the cool moist climate at Pine Mountain may have limited the survival of larvae in many bee species by increasing the susceptibility of nest provisions to mold and by slowing bee development, thereby lengthening the mold-sensitive period (Linsley 1958).

The tendency for most bees to reach peak numbers on the shrubs around midday may reflect primarily their need to restrict their flower-visiting activity to daytime hours when temperature and insolation are appropriately high (Linsley 1958, 1978; K pyl  1974; Willmer 1983) and secondarily the temporal pattern of nectar and pollen availability in the flowers. Depletion of food rewards was probably the main cause behind the sharp decrease in bees after early afternoon. The unimodal pattern of daily activity was strongest among the smaller bees; in progressively larger and more hairy bees, this pattern became less pronounced and eventually bimodal (*Bombus* and large Anthophoridae). Similar observations of bees visiting *Lavendula* were shown to relate to differences in body size and were correlated with the bees' differing temperature requirements for flight and nectar-water needs (Herrera 1990). It has certainly been repeatedly noted that the composition of bee species at a flower source changes during the day, with the most energetically demanding bees arriving first (Roubik 1989). On a seasonal level, in mediterranean Israel the body sizes of bees are reported to correlate negatively with the seasonal increase in air temperature (Shmida & Dukas 1990), but such trends were not evident in the present study with the possible exception of *Hylaeus*,



which, unlike other small-sized bee groups, showed a general increase in numbers of species over the course of the study.

The relatively open vegetation of both shrubs and trees in the area at Pine Mountain contrasted with the more dense and heterogeneous woody vegetation at Mt. Veeder, and although availability of nesting locations for ground-nesting bees was probably comparable at the two sites, conditions for twig- and cavity-nesting bees may have been more limiting at Pine Mountain. Potentially vulnerable bees included Megachilidae, as well as wood-nesting species in Anthophoridae (*Ceratina* and *Xylocopa*) and Colletidae (*Hylaeus*) (Stephen et al. 1969). However, even in these cases, climate may have been the most restricting factor (P. F. Torchio, personal communication).

Flowering shrubs were the principal food source for the bees collected at both sites, based on field observations and on analysis of female pollen loads, although some bees at Mt. Veeder did visit other plants in low frequency (Dobson 1980). The shrub floras were similar between sites, and differed mainly in their respective species of *Arctostaphylos* and *Ceanothus*, making it unlikely that shrub composition was a major determinant of the sites' different bee faunas. However, shrub cover and consequently food density, which has been shown to influence levels of bee foraging activity (Moldenke 1975, Ginsberg 1983, Sih & Baltus 1987), was less at Pine Mountain and probably contributed to the lower abundance of bees. The effect of shrub cover on bee species richness is less clear, but the marked increases in bee species during 1978 when shrub bloom was denser (particularly at Mt. Veeder) suggests that it too may have been a factor in the disparate number of bee species between sites.

The diversity of bees visiting the different shrubs underscores the importance of all shrub species in providing food for the resident bees. In turn, most chaparral shrub species are self-incompatible and depend upon insects for pollination (Keeley & Keeley 1988). Each shrub was visited by a distinctive spectrum of bee species from different families. *Ceanothus* species and *H. arbutifolia*, covering the beginning and end of the spring season respectively, attracted the greatest diversity. Both genera have bowl-shaped flowers where the nectar and pollen are easily accessible to a variety of insects. Curiously, *A. fasciculatum*, which has small bowl-shaped flowers and is the most common shrub in the California chaparral, received very low visitation. These patterns are not, however, consistent across chaparral sites in California (Moldenke & Neff 1974c; A. R. Moldenke, personal communication). At some locations, high bee diversities have been observed on additional shrubs, including *Arctostaphylos* species, which were not fully sampled in the present study; and although the paucity of bees on *A. fasciculatum* corroborates observations in other northern California sites (i.e., at Jasper Ridge and Mather), in certain areas, particularly southern California, bee diversity may reach very high levels. *Ceanothus* species, however, number regularly among the chaparral shrubs attracting the greatest diversity of bees.

Certain bee families showed definite seasonal patterns in their numbers of species and were consequently more frequent visitors on some shrubs than on others, although shrub-choice was undoubtedly also influenced by accessibility and quantity of food rewards. Thus, the early-season Andrenidae visited almost exclusively *Arctostaphylos* and *Ceanothus*, as reported in other chaparral areas (Moldenke & Neff 1974b), whereas Megachilidae, which reached peak numbers

at mid-season and are relatively long-tongued, foraged mainly on *Eriodictyon*, *Mimulus*, and *Pickeringia*.

Reasons behind the differing proportions of male bees at Pine Mountain compared to Mt. Veeder are not clear, although sex ratios can vary considerably both inter- and intraspecifically (Stephen et al. 1969, Michener 1974, Roubik 1989). One factor possibly involved is the phenomenon of protandry, in which males emerge up to a week or more prior to females (and females generally outlive males). Although Linsley (1958) points out that some reports of protandry may in fact reflect the earlier activity of males on flowers rather than any actual earlier emergence, protandry appears to be prevalent in most families of bees except Halictidae and Apidae (social species), which tend to produce males at the end of the season (Robertson 1918, 1930). The remarkably low proportion of male Andrenidae at Mt. Veeder may thus have resulted from the study being initiated after the emergence of males but during the peak activity time of females. Indeed, flower visitors on the early-blooming *Arctostaphylos* shrubs, which males appeared to use as their principal food source, were not sampled throughout their entire bloom period. At Pine Mountain, where the spring season was a little later, the *Arctostaphylos* bloom was fully included in the study and the proportion of Andrenidae males reached much higher levels, close to 50%. In the case of bumble bees, however, it is the factor of early-season nest establishment that underlies the higher proportion of *Bombus* males at Mt. Veeder, most of which were *B. edwardsii*. This species, which was poorly represented at Pine Mountain, as well as *B. vosnesenskii* may establish nests in winter and produce males in early spring (Linsley 1944, Thorp et al. 1983).

Besides timing of flight activity, several other factors may have influenced the variation in sex ratios of collected bees, both within and between sites. First, males and females may differ in the flowers they visit and thus in their tendency to frequent shrubby species. Second, species-specific mating strategies and the associated sites for mate location (e.g., at food sources, near nests, or elsewhere) may result in differing abundances of males and females on the blooming shrubs. Finally, males and females may vary in their wariness of any disturbance created by the collector near the flowers (D. M. Gordon, personal communication) and in the ease with which they are collected; these last factors may also create a bias in the relative abundances of species based on collection data.

Observations of negative interactions between honey bees and solitary bees on selected shrubs suggest that honey bees may substantially influence the foraging activities of native chaparral bees and that they may be competing with them for floral resources. The aggressive chasing away of smaller bees by honey bees was similar to that reported in other bees (e.g., Frankie 1976) and did not appear to reach the high levels of aggression described in eusocial bees (Roubik 1989). The less aggressive displacement of solitary bees through their avoidance of honey bees landing on their flowers may be a relatively common behavior in encounters involving social bees of differing size or aggressivity (Johnson & Hubbell 1975, Morse 1977, Roubik 1989). Although effects of honey bees are difficult to quantify, data gathered by Schaffer et al. (1983) suggest that honey bees compete with native bees (including bumble bees) by reducing the available nectar and evidence from other studies imply that they can have a major impact on the population dynamics and foraging activities of solitary bees (Eickwort & Ginsberg 1980, Ginsberg 1983).



The present study points to the variation in bee faunas that can occur in similar plant communities lying within short distances of each other and to the apparently strong influence that climatic conditions may have in shaping bee diversity and abundance. Given the compositional differences in bee faunas between the 2 years, extension of the study over a broader seasonal span would provide further insight in the population dynamics of native bees in these chaparral areas. In addition to contributing to our understanding of chaparral insects (Force 1990), the data herein could serve as a baseline for future sampling of chaparral bee faunas. From the perspective of biological conservation, insect faunal monitoring is of prime importance if we wish to evaluate any changes in a community incurred from habitat (vegetation) changes, human disturbance, or introduced species. Yet, insects have been generally underrepresented in biotic inventories and local insect surveys are wanting (Disney 1986, Wilson 1987). The paucity of attention given to native bees, which are important pollinators of indigenous plants and thus key components of communities, needs to be redressed (Osborne et al. 1991). With this goal in mind, the information here could assist in the effective protection and preservation of the California chaparral and its associated insect fauna.

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Appendix 1. Bee species collected on the flowers of chaparral shrubs at the Mt. Veeder (V) and Pine Mountain (P) sites, 1977 and 1978, with total number of specimens collected (males and females).

Bee species	Host-shrub genera <sup>a</sup>									No. bees <sup>b</sup>	
	Arct	Cean	Dend	Erio	Mimu	Pick	Rham	Aden	Hete	V	P
<b>ANDRENIDAE</b>											
<i>Andrena angustitarsata</i> Viereck	V	V					P			11C	1A
<i>Andrena astragali</i> Viereck & Cockerell		P								—	1A
<i>Andrena auricoma</i> Smith		V								1A	—
<i>Andrena candidiformis</i> Viereck & Cockerell	V	VP								27C	1A
<i>Andrena chlorogaster</i> Viereck		V								4C	—
<i>Andrena chlorura</i> Cockerell	VP	VP		V			P			49C	4B
<i>Andrena cristata</i> Viereck	V									2B	—
<i>Andrena fuscicauda</i> (Viereck)		V					P			4A	1B
<i>Andrena obscuripostica</i> Viereck		V								3B	—
<i>Andrena orthocarpus</i> Timberlake		V								6C	—
<i>Andrena prolixa</i> LaBerge		VP								3A	2B
<i>Andrena salicifloris</i> Cockerell		V								1B	—
<i>Andrena transnigra</i> Viereck	V									1B	—
<i>Andrena vandykei</i> Cockerell	VP	VP								96C	6C
<i>Andrena w-scripta</i> Viereck		V								10C	—
<i>Panurginus atriceps</i> (Cresson)		V	V							28C	—
<i>Panurginus gracilis</i> Michener		P								—	5B
<i>Panurginus nigrellus</i> Crawford	P									—	21B
<b>ANTHOPHORIDAE</b>											
<i>Anthophora pacifica</i> Cresson	V									1B	—
<i>Anthophora urbana</i> Cresson						V				2B	—
<i>Ceratina acantha</i> Provancher				V	V					13C	—
<i>Ceratina arizonensis</i> Cockerell									V	1B	—
<i>Ceratina nanula</i> Cockerell		P							V	—	1A
<i>Ceratina punctigena</i> Cockerell					V					1B	—
<i>Emphoropsis depressa</i> (Fowler)	VP	VP		VP						9C	2C
<i>Nomada</i> undet.	VP	VP					V			20C	2C
<i>Xylocopa tabaniformis</i> var <i>orpifex</i> (Smith)	V				V	V				10C	—



Bee species	Host-shrub genera <sup>a</sup>									No. bees <sup>b</sup>	
	Arct	Cean	Dend	Erio	Mimu	Pick	Rham	Aden	Hete	V	P
<b>APIDAE</b>											
<i>Apis mellifera</i> (Linnaeus)	VP	VP		V		V	VP	VP	VP	C <sup>c</sup>	C
<i>Bombus californicus</i> Smith									V	2B	—
<i>Bombus caliginosus</i> (Frison)	P	V		VP	V	V		V	V	22C	14C
<i>Bombus edwardsii</i> Cresson	V	VP		VP		V				70C	4C
<i>Bombus flavifrons</i> (Ashmead)		V								1B	—
<i>Bombus vosnesenskii</i> Radoszkowski		V		VP		VP	P		VP	9C	12C
<b>COLLETIDAE</b>											
<i>Hylaeus calvus</i> (Metz)		V		V			VP		V	22C	8C
<i>Hylaeus episcopalis</i> (Cockerell)				V		V	VP	V	V	28C	1B
<i>Hylaeus modestus citrinifrons</i> (Cockerell)								VP		1B	1B
<i>Nylaeus nevadensis</i> (Cockerell)									V	1B	—
<i>Hylaeus nunenmacheri</i> Bridwell		V		V						21C	—
<i>Hylaeus (Paraprosopis) undet.</i>									V	1B	—
<i>Hylaeus polifolii</i> (Cockerell)		VP		VP	V		VP	VP	VP	48C	37C
<i>Hylaeus rudbeckiae</i> (Cockerell & Casad)									VP	3B	4B
<i>Hylaeus verticalis</i> (Cockerell)		V		V	V	V	V		V	32C	—
<b>HALICTIDAE</b>											
<i>Dialictus</i> sp. 20	P			VP	V	V	V			12C	2B
<i>Dialictus incompletus</i> (Crawford)	V		V				P		P	2B	4C
<i>Dialictus nevadensis</i> (Crawford)		VP	V	P	V		V	VP	VP	21C	6C
<i>Dialictus punctatoventris</i> Crawford							V		V	4C	—
<i>Dialictus tegulariformis</i> (Crawford)	P			P				P		—	3B
<i>Dialictus undet.</i>									VP	2B	2A
<i>Evylaeus argemonis</i> (Cockerell)	V					V	P	VP		4B	2B
<i>Evylaeus nigrescens</i> (Crawford)	P	V		P			P	VP	VP	9C	14C
<i>Evylaeus near synthyridis</i>	P	V				V				3C	2B
<i>Evylaeus undet.</i>						V		V	P	3B	1B
<i>Halictus tripartitus</i> Cockerell	P	VP		VP		V		V	VP	26C	10C
<i>Halictus (Seladonia) undet.</i>									P	—	1A
<i>Lasioglossum mellipes</i> (Crawford)					V				P	2B	2B

Bee species	Host-shrub genera <sup>a</sup>									No. bees <sup>b</sup>	
	Arct	Cean	Dend	Erio	Mimu	Pick	Rham	Aden	Hete	V	P
<i>Lasioglossum sisymbrii</i> (Cockerell)							P			—	1B
<i>Sphecodes</i> sp. 1									V	2B	—
<i>Sphecodes</i> sp. 2								V		1B	—
MEGACHILIDAE											
<i>Callanthidium illustre</i> (Cresson)						V				1B	—
<i>Chelostomopsis rubifloris</i> (Cockerell)	P	V		V	V	V				15C	1B
<i>Dianthidium plenum</i> Timberlake						P				—	1A
<i>Heriades occidentalis</i> Michener									V	5C	—
<i>Hoplitis producta gracilis</i> (Michener)				V						1B	—
<i>Hoplitis sambuci</i> Titus				V		V			V	13C	—
<i>Megachile b. brevis</i> Say									V	1A	—
<i>Megachile gemula</i> (Cresson)						V				1B	—
<i>Megachile gentilis</i> Cresson									V	1B	—
<i>Megachile (Leptorachis) undet.</i>									V	1A	—
<i>Osmia a. albolateralis</i> Cockerell						V				3B	—
<i>Osmia b. brevis</i> Cresson						V				4A	—
<i>Osmia bruneri</i> Cockerell				V						6C	—
<i>Osmia cobaltina</i> Cresson					V	V				8C	—
<i>Osmia cyanella</i> Cockerell					V	V	V			12B	—
<i>Osmia exigua</i> Cresson				V	V					2C	—
<i>Osmia gabrielis</i> Cockerell					V	V				7C	—
<i>Osmia juxta</i> Cockerell				V	V					3B	—
<i>Osmia lignaria propinqua</i> Cresson	V	V		V						9C	—
<i>Osmia ribifloris biedermaunii</i> Michener	V									2B	—
<i>Osmia tristella</i> Cockerell		V		V	V				V	6C	—
<i>Osmia (Chenosmia) undet.</i>		V		V	V					5C	—
<i>Trachusa gummifera</i> Thorp						V				4B	—

<sup>a</sup> Shrub genera; Arct = *Arctostaphylos*, Cean = *Ceanothus*, Erio = *Eriodictyon*, Dend = *Dendromecon*, Mimu = *Mimulus*, Pick = *Pickeringia*, Aden = *Adenostoma*, Hete = *Heteromeles*. See text for species names.

<sup>b</sup> Year of collection: A = 1977 only, B = 1978 only, C = both 1977 and 1978.

<sup>c</sup> Specimen number not specified, since bees not collected in representation of abundance.